Long-term changes in forest composition and diversity following early logging (1919–1923) and the decline of American chestnut (*Castanea dentata*)

Katherine J. Elliott · Wayne T. Swank

Abstract Chestnut blight fungus (*Endothia parasitica* [Murr.] P.J. And. & H.W. And.)) is a classic example of an invasive species, which severely damaged populations of its host, *Castanea dentata*, and had widespread and long-term impacts on eastern North American forests. Concurrently, forests were further disturbed by lumbering, which was common across the region from the mid 1800s to the early 1900s. In 1926, local infestations of chestnut blight were reported in the Coweeta Basin, Southern Appalachian Mountains of North Carolina. We used permanent plot inventories of the Basin (first sampled in 1934 and twice afterward in 1969–72 and 1988–93) to describe the distribution of species along a complex environmental gradient. Specifically, we asked: How does vegetation change over approximately 60 years following logging and the demise of *C. dentata?* Does the association between vegetation and environment determine the pattern of species distributions through time? Which species replaced *C. dentata* across this complex environmental gradient? We used nonmetric multidimensional scaling ordination and multiresponse permutation procedure for the analyses of the inventory periods. In 1934, *C. dentata* was the most important species in the Coweeta Basin. It was present in 98% of the plots and contributed 22% of the total density and 36% of the total basal area. Diversity increased significantly over time and was attributed to an increase in evenness of species distribution. The canopy dominant, *C. dentata*, was replaced by more than one species across the environmental gradient. Importance values of *Quercus prinus*, *Acer rubrum*, *Cornus florida*, *Tsuga canadensis*, and *Oxydendrum arboreum* increased by 2–5% across the basin following the decline of *C. dentata*. *Tsuga canadensis* increased in abundance and distribution, especially near streams across elevations. *Liriodendron tulipifera* replaced *C. dentata* in moist coves, which have low terrain shape and high organic matter content. In contrast, *Q. prinus* and *A. rubrum* were ubiquitous, much like *C. dentata* before the chestnut blight becoming dominant or co-dominant species across all environmental conditions.

Keywords *Quercus prinus* · *Quercus rubra* · *Tsuga canadensis* · Disturbance · Disease pandemic · Long-term data

K. J. Elliott (✉) · W. T. Swank
Forest Service, US Department of Agriculture, Coweeta
Hydrologic Laboratory, Southern Research Station, 3160
Coweeta Lab Rd, Otto, NC 28763, USA
e-mail: kelliott@fs.fed.us

Introduction

In forested ecosystems throughout the world, tree species are disappearing due to introductions and subsequent outbreaks of exotic pests and pathogens, irruptions of native pests, logging, and deliberate removals of single species (Ellison et al. 2005). The loss of tree species from North American forests is resulting in fundamental shifts in population and community dynamics of associated species and immediate and long-term changes in ecosystem dynamics (Ellison et al. 2005). Chestnut blight fungus (*Cryphonectria parasitica* (Murr.) Barr (= *Endothia parasitica* [Murr.] P.J. And. & H.W. And.)), a classic example of an invasive species, had widespread and long-term influences on eastern North American forests (Day and Monk 1974; Shugart and West 1977; Ellison et al. 2005). This fungus disease devastated the former oak-chestnut forest association (Braun 1950) by eliminating the dominant or co-dominant *Castanea dentata*.

Castanea dentata was a dominant species in the upland forest communities of much of eastern North America, until it was virtually eliminated by chestnut blight at the beginning of the 20th century. Chestnut blight, caused by the bark-inhabiting canker fungus, was introduced from Asia in the late 19th century (Milgroom et al. 1996). The blight was first discovered in New York in 1904, spread rapidly ($\sim$37 km yr^{-1}) across the range of chestnut, and within 50 years had converted this stately tree to a rarely flowering understory shrub across $\sim$3.6 million ha of chestnut forest (Anagnostakis 1987). Areas were further disturbed by lumbering and fire, which frequently followed the blight (Brose et al. 2001).

Reconstructing forest dynamics following chestnut blight is challenging because it requires information on forest structure and composition pre- and post-blight. For most historical invasions, such as the chestnut blight, good baseline data on the distribution and abundance of the species assemblages are rare, and little to no information on basic ecosystem processes is available. Although various studies provided an indication of early regeneration for a variety of sites ranging from New England to Tennessee and North Carolina (Korstian and Stickel 1927; Braun 1940; Keever 1953; Nelson 1955; Woods and Shanks 1957, 1959; Good 1968), most of these studies were completed within the first 20 years after the blight infected a region. Several studies were conducted in other regions of the United States (Korstian and Stickel 1927; Aughanbaugh 1935; Good 1968; Mackey and Sivec 1973) and in the Southern Appalachians (Keever 1953; Nelson 1955; Woods and Shanks 1959; Shugart and West 1977; McCormick and Platt 1980) to examine the replacement of chestnut following the chestnut blight in the 1920s. To our knowledge, records of pre-blight vegetation are available only for the Connecticut plots of Korstian and Stickel (1927). The characteristics of pre-blight vegetation could be reconstructed for permanent plots sampled in Virginia in 1939 (McCormick and Platt 1980) and for plots sampled in Pennsylvania in 1934 (Aughanbaugh 1935). Most studies have been confined to investigations of forests after the elimination of chestnut by reconstruction of the pre-blight forest using existing chestnut stumps as a reference (Woods and Shanks 1959; Good 1968; Karban 1978; Van Lear et al. 2002; Myers et al. 2004) or public land records that recorded trees at boundaries or corners (McEwan et al. 2005).

In 1926, local infestations of chestnut blight were reported in Western North Carolina and North Georgia (Gravatt and Marshall 1926; Keever 1953); and it was first noted in the Coweeta Basin. Soon after establishment of Coweeta Hydrologic Laboratory as an experimental forest administered by USDA Forest Service, vegetation surveys were initiated along permanent transects across the Basin. One vegetation survey occurred in 1934–35 and included measurements of standing, infected and dying *C. dentata*. This survey provides a basis for reconstructing the forest structure, composition, and diversity prior to the chestnut blight in the Southern Appalachians. Data from later inventories on these same permanent plots afford a unique opportunity to assess what species have replaced *C. dentata* along an environmental gradient. Our study area, a 1,626 ha basin, is larger and more environmentally varied than those examined previously, and the period covered by our observations (ca. 60 years) is longer than those in other studies.

The biological significance of invasive species can have effects on five levels: (1) individuals (mortality and growth), (2) genetic (including hybridization), (3) population abundance and dynamics, (4) community effects (diversity, trophic structure), and (5) ecosystem processes (primary productivity, nutrient

cycling) (Parker et al. 1999). Our goal is to address how chestnut blight fungus impacted individuals, population abundance, and community diversity and composition. We also offer brief comments on how chestnut blight impacted genetic diversity and ecosystem processes. Our objectives were to: (1) examine the change in vegetation over approximately 60 years in a southern mixed deciduous forest following logging and the demise of *C. dentata*, (2) investigate the association between the vegetation and the abiotic and physical site variables that determine the pattern of species distribution through time, and (3) determine which species replaced *C. dentata* across this complex environmental gradient.

Methods

Study area

Coweeta Hydrologic Laboratory is a research site of the USDA Forest Service, Southern Research Station. It is located in the Nantahala Mountain Range of Western North Carolina, USA, within the Blue Ridge Physiographic Province, near the southern end of the Appalachian Mountain chain (latitude 35°03′ N, longitude 83°25′ W). The 2,185 ha laboratory consists of two adjacent, east-facing, bowl-shaped basins; Coweeta Basin and Dryman Fork Basin. The Coweeta Basin encompasses 1,626 ha and is drained by Ball Creek and Shope Fork, two fourth-order streams. These streams join to form Coweeta Creek, which flows 7 km east to the Little Tennessee River. The vegetation survey did not include Drymans Fork, a 559 ha basin, since it was not added to the laboratory until 1946. Elevations range from 675 to 1,592 m. Slopes are steep ranging from 30 to over 100%. Soils are deep sandy loams and are underlain by folded schist and gneiss. Two soil orders are found within Coweeta, immature Inceptisols and older developed Ultisols (Thomas 1996). The relief has a major influence on hydrologic, climatic, and vegetation characteristics. Streams flow throughout the year, fed by approximately 2,000 mm of precipitation per year, most of which is rain. Mean annual temperature is 12.6°C and ranges from an average of 11.7°C in winter to 21.6°C in summer. Frequent rain, more than 130 storms distributed throughout the year, sustains high evapotranspiration rates and a humid climate

(Swift et al. 1988). Vegetation is southern mixed deciduous forest. The principal overstory species are of the genera *Quercus*, *Carya*, and *Liriodendron*. There are scattered groups of *Pinus rigida* and *Tsuga canadensis*. Evergreen shrubs (*Rhododendron* and *Kalmia*) combine with *Cornus*, *Robinia*, *Acer*, and *Betula* to form a dense understory cover (Day et al. 1988).

Disturbance history

The Basin was part of the Cherokee Indian Nation until the Nation was moved in 1837. The Cherokee practiced semiannual burning to improve forage for livestock (Douglass and Hoover 1988). In 1842, Charles Dryman built the first house on the present administrative area. Between 1842 and 1900, European settlers continued the practice of light semiannual burning and grazing. The Forest Service purchased the Basin in 1918, but rights to timber over 38 cm (15 inches) at the stump were reserved for the J.A. Porter Logging Company. Logging began in 1919, and selective but heavy cutting continued until 1923. By 1923, when the Forest Service took over administration of the Coweeta Basin, 8 million board feet of timber had been removed (Douglas and Hoover 1988).

Chestnut blight was first noted in Coweeta in the early 1920s. In the decades between 1970 and 1990, two large-scale, natural disturbances have been documented. Dogwood anthracnose, caused by *Discula destructiva* Redlin, average incidence of infection of *Cornus florida* was 87% by 1990 in the Coweeta Basin (Chellemi et al. 1992). A major drought was recorded from 1985–88 in the Coweeta Basin (Swift et al. 1989). Clinton et al. (1993) showed that there was an increase in canopy gap formation due to hardwood tree mortality and significant mortality of *P. rigida* occurred due to a combination of drought and subsequent attack by the southern pine beetle (*Dendroctonus frontalis* Zimmerman) (Smith 1991).

Vegetation surveys

Permanent plots were used to study changes in forest vegetation patterns over a 60-year-period at Coweeta;

987 permanent plots were inventoried during 1934–1935 (hereafter 1934), 403 of the original permanent plots were re-inventoried during 1969–1973 (hereafter 1970s), and 297 permanent plots were re-inventoried during 1988–1993 (hereafter 1990s). Only data from the 281 permanent plots that were re-inventoried during all three periods (1934, 1970s, and 1990s) were used in our analyses. These 281 plots were located in reference watersheds, which have been without human disturbance since 1923 (Douglass and Hoover 1988). Permanent 0.08 ha (20 m × 40 m) plots were established along 13 parallel, approximately North–South transects (330°) spanning the Coweeta Basin at 200 m intervals. Chestnut stakes were used to establish plot corners in 1934 and most of these stakes were still standing in the 1970s inventory. Subsequently, plot corners have been referenced with pvc pipe. Trees > 1.37 m height and ≥ 2.5 cm dbh (diameter at 1.37 m height) were tallied by species in 2.5 cm diameter classes in each plot. The 1934 survey included diameter classes for live but blight infected *C. dentata* (no notes were taken as to the condition of the standing *C. dentata* trees). Diameter class of cut stumps was recorded for trees harvested during the 1919–1923 logging operations. Cut stumps were not identified to species on the 1934 survey sheets. For all species and inventories, we calculated frequency, density (number of stems per hectare), relative density (number of stems of a given species as a proportion of total number of stems of all species), basal area (m^2/ha), relative basal area (basal area of a given species as a proportion of total basal area of all species), and importance value (IV; {relative density + relative basal area} ÷ 2). We also calculated the density and basal area of cut stumps that were measured in the 1934 inventory. Plant species nomenclature follows Kirkman et al. (2007).

Site variables

Site variables used in our analyses included percent slope, elevation, modified azimuth, terrain shape, soil depth, depth of A-horizon, soil clay content, soil organic matter content, mean temperature during the growing season, growing season precipitation, and potential solar radiation. Values of site variables were determined by direct measurements or calculated by digital geographical information system (GIS) mapping methods (Elliott et al. 1999). During the 1970s survey, percent slope, aspect, elevation, and slope position (ridge, upper slope, middle slope, lower slope, or cove) were recorded for each plot. Terrain shape, mean temperature, and potential solar radiation were derived using a GIS (ARC/INFO[tm]).[1] Soils data for individual plots were obtained from a first-order soil survey completed in 1985 by the Natural Resources Conservation Service (Thomas 1996). This soil survey map was overlain onto the permanent vegetation plots map using a GIS (ARC/INFO[tm]). Maximum values for percent soil organic matter content, percent clay content, soil water content, soil depth, and depth of A-horizon were derived from soil series descriptions and used in our analyses.

Previous research at Coweeta has shown that the above site variables modify the local environment. Plot soil moisture is a function of precipitation (input), terrain shape (water drainage), and soil characteristics (water holding capacity) (Yeakley 1993). Availability of soil nutrients is a complex function of soil characteristics including organic matter content, clay content, soil depth, A-horizon depth, terrain shape (affecting downslope movement of nutrients with water drainage), and soil temperature and moisture (Knoepp and Swank 1997a, b). Temperature is a function of elevation, terrain shape (e.g., ridge, middle slope, or cove bottom), aspect (e.g., south-facing slope or north-facing slope), and percent slope. Potential solar radiation, adjusted for solar declination (latitude), at any plot is influenced by the slope inclination and aspect, shading by adjacent hills, and cloud cover (Swift and Knoerr 1973).

Digital terrain shape was determined by taking a scaled 9-celled zero-sum difference, centric minus the weighted average of perimeter cells (Burrough 1986; McNab 1989), using a GIS (ARC/INFO[tm]). This yielded an unitless value for each ground position. Calculated values for terrain shape were rescaled linearly, where the range −2 to +2 was rescaled from 0 (highest concavity–deep coves) to 10,000 (highest convexity–narrow, well-defined ridges).

---

[1] The use of trade or firm names in this publication is for reader information and does not imply endorsement by the US Department of Agriculture of any product or service.

For each plot, mean temperature during the growing season was calculated by means of a temperature prediction model (Bolstad et al. 1998b). Temperatures decreased with elevation at mean rates of 7°C km^{-1} (maximum temperature) and 3°C km^{-1} (minimum temperature); growing season temperature range was 16.8–22.0°C. Mean annual precipitation for each plot was estimated on the basis of long-term data and isohyetal maps that provide weighting factors (Swift 1968); mean annual precipitation range was 177–255 cm. Solar radiation on mountain slopes was estimated using an algorithm for calculating potential radiation (Swift and Knoerr 1973; Swift 1976). This algorithm estimates solar radiation within 10% of measured radiation values when slope, aspect, and a variable to adjust for topography are included; potential solar radiation range was 42–131%.

Data analyses

We evaluated species diversity using species richness (S), Shannon-Wiener's index of diversity (H′), and species evenness (E). Shannon-Wiener's index incorporates both species richness and the evenness of species abundance (Magurran 2004). H′ and E were calculated at the plot level and averaged for each survey period. We used repeated measures ANOVA (PROC GLM, SAS 1999) to determine significant differences in density, basal area, and diversity (S, H′, and E) among inventory periods.

To examine the relationships among tree species composition and environmental variables, we used separate nonmetric multidimensional scaling (NMS) (Clarke 1993; McCune and Mefford 1999; McCune and Grace 2002) ordination analyses for each inventory period (1934, 1970s, and 1990s). In addition, vegetation data were combined for all three inventory periods into one NMS ordination analysis to examine how sample plots moved across ordination space through time. We used tree species basal area as the measure of abundance in the NMS analyses. With NMS, we explored the vegetation–environment relationships among tree species abundance (basal area) and site characteristics. NMS was conducted using the Sorensen distance measure with 60 runs of real data and 50 runs of randomized data (with a maximum of 200 iterations for each run). A three-dimensional solution was chosen for the final iterative

ordination, and the best ending point in the preliminary analysis was used as the starting point in the final run. We report the final stress of the ordination and coefficients of determination (R^2) for each ordination axis calculated as a proportion of the variation explained in the reduced matrix relative to that in the original matrix. Ecological community data sets often have final stress values between 10 and 20, and values in the lower half of this range indicate reliable solutions (McCune and Grace 2002).

A secondary matrix of site environmental variables (percent slope, elevation, terrain shape index, modified azimuth, soil organic matter content, soil clay content, soil depth, soil A-horizon depth, air temperature, solar radiation, annual precipitation, and basal area of cut stumps) was used to help interpret the ordination results. We chose to include basal area of cut stumps in our NMS analysis as an indicator of harvesting disturbance level. In the resulting ordination graph, plot points indicate sites and line-vectors indicate environmental variables. The length of each line-vector represents the rate of change in the weighted average as inferred from the biplot, showing how much the species distributions and sites differ along that environmental variable. The most important variables are those with the longest line-vector. Monte Carlo permutations were applied to NMS analyses to determine if the strength of species sorting along the environmental variable was greater than would be expected by chance ($P < 0.020$) (ter Braak 1986; Crowley 1992). We chose to graph only the environmental variables with an $R^2 \geq 0.15$.

We used the "proportion of max" feature in PC-ORD and rotated the diagrams using terrain shape in the secondary matrix to create better uniformity among the NMS graphical displays of the three inventory periods. To compare tree species composition among the inventory periods (1934–1935, 1969–1972, and 1988–1993), we used a multiresponse permutation procedure (MRPP) (McCune and Mefford 1999; McCune and Grace 2002). MRPP is a nonparametric multivariate test of differences between a priori groups (Mielke 1991), which provides a T-test statistic and a P-value. A stronger separation between groups is reflected by a more negative T-statistic. We compared Sørensen distance and Euclidean distance (with and without ranking). Since these distances showed similar results and Sørensen distances are less prone to exaggerate the

influence of outliers (McCune and Grace 2002), we are reporting on Sørensen distance without ranking. When comparisons across inventory periods were significant, we applied multiple pair-wise comparisons using Sørensen distance. We used PC-ORD version 4 (McCune and Mefford 1999) for the NMS ordination analyses and MRPP group separation tests.

Results

In the 1934 survey, *C. dentata* was the most important species in the Coweeta Basin. It was present in 98% of the plots and contributed 22% of the total density and 36% of the total basal area (Table 1). The species that ranked highest in importance value in 1934 were *C. dentata* > *Q. prinus* > *A. rubrum* > *C. florida* > *Carya* spp. (Table 1). In the 1970s survey, species were ranked in the order *Q. prinus* > *A. rubrum* > *C. florida* > *Q. coccinea* > *Carya* spp., and *C. dentata* was ranked eighth. By the 1990s, species were ranked in the order *A. rubrum* > *Q. prinus* > *C. florida* > *Q. coccinea* > *Carya* spp., and *C. dentata* was ranked twelfth. Although *C. dentata* was present in 61% of the plots, its basal area was less than 1.0% of the total (Table 1). *Tsuga canadensis* occurred in only 16% of the plots in 1934; by the 1990s inventory it occurred in 50% of the plots and its basal area had increased by more than 400% (Table 1).

Tree density was significantly higher in 1934 than in the other two inventory periods (Table 2). Average basal area of the forest at the time of the first survey was only 28.0 m^2 ha^{-1} (Table 2). By the 1990s, basal area had increased significantly, to 30.1 m^2 ha^{-1}. In 1934, cut stumps averaged 7.0 m^2 ha^{-1} and basal area removed from individual plots ranged from 0 to 52 m^2 ha^{-1}. Only two plots had no cut stumps, 40% of the plots had ≥5.0 m^2 ha^{-1}, and 24% of the plots had ≥10.0 m^2 ha^{-1} of basal area removed. $H'_{basal\ area}$ was significantly higher in the two later inventories than in 1934, but species richness did not significantly decrease until the 1990s (Table 2).

In 1934, size class distribution of species indicated that the forest was experiencing high recruitment of small stems (2.5–7.5 cm dbh) (Fig. 1). *Castanea dentata* had a high number of small stems, and it had more stems in all size classes than any other co-occurring species (Fig. 1). After 1934, the number of

large size-class stems decreased for *C. dentata*, with <1.0 stems ha^{-1} for size classes ≥15.0 cm dbh (Fig. 1), and the number of small stems (those <15 cm dbh) had decreased by 75% in the 1970s and 90% in the 1990s. *Acer rubrum* had many stems in the small size-classes (<15.0 cm dbh) in all survey periods, but an increasing number of large stems in the 1970s and 1990s (Fig. 1). *Liriodendron tulipifera* had fewer small size-class stems through time and an increasing number of larger stems by the 1970s (Fig. 1). *Tsuga canadensis* had more stems in all size-classes in the 1970s and 1990s than in 1934 (Fig. 1), and this demonstrates the recruitment and growth of this species after the demise of *C. dentata*.

The NMS ordination for the 1934 data (Fig. 2a) converged on three axes for the final solution (McCune and Mefford 1999). The final stress for the three-dimensional solution was 15.06. The proportion of variance explained was 19% for Axis 1, 37% for Axis 2, and 30% for Axis 3 (cumulative $R^2 = 86.5\%$ for the first three ordination axes) (Table 3). When the secondary matrix of site environmental variables was examined, Axis 2 was positively correlated with terrain shape and annual temperature and negatively correlated with basal area of cut stumps, soil organic matter, and A-horizon depth (Table 3, $R ≥ 0.30$). Axis 3 was positively correlated with elevation and annual precipitation and negatively correlated with solar radiation (Fig. 2a, Table 3). In the NMS ordination diagram, tree species that were most positively related to Axis 1 were *Q. prinus* and *Q. coccinea* (Table 4, tau ≥ 0.30); and species most negatively related were *C. dentata* and *Carya* spp. (Fig. 2a, Table 4). Species most positively related to Axis 2 were *Q. coccinea*, *Castanea pumila*, *P. rigida*, and *Q. prinus*; and species most negatively related were *B. lenta*, *L. tulipifera*, *Hamamelis virginiana*, *Fraxinus americana*, *Q. rubra*, *A. pensylvanicum*, *Tsuga canadensis*, *Cornus florida*, *A. rubrum*, and *Tilia americana* (Fig. 2a, Table 4). Species most positively related to Axis 3 were *C. dentata*, *Q. prinus*, and *Q. rubra*; and species most negatively related were *Q. alba* and *Q. velutina* (Fig. 2a, Table 4).

The NMS ordination for the 1970s data (Fig. 2b) converged on three axes for the final solution (McCune and Mefford 1999). The final stress for the three-dimensional solution was 15.49. The proportion of variance explained was 17% for Axis 1,

Table 1 Percent frequency ($n = 281$), density (stems ha^{-1}), basal area (BA; m^2 ha^{-1}), and importance value (IV; (relative density + relative basal area) ÷ 2) for 1934–1935, 1969–1972, and 1988–1993 tree inventories of the Coweeta Basin

Species	1934–1935				1969–1972				1988–1993			
	Freq	Density	BA	IV	Freq	Density	BA	IV	Freq	Density	BA	IV
Castanea dentata	98	686	10.08	29.0	80	152	0.39	4.8	61	66	0.16	2.6
Quercus prinus	89	246	3.43	10.1	89	181	5.48	15.0	89	118	6.32	14.6
Acer rubrum	95	339	1.50	8.1	100	299	2.69	12.9	99	256	4.13	16.1
Quercus coccinea	73	172	2.61	7.4	68	82	3.31	8.3	59	47	2.59	5.9
Carya spp.	88	272	1.60	7.2	85	141	1.77	7.0	80	79	1.74	5.7
Cornus florida	77	234	0.63	4.9	82	284	0.93	9.3	75	192	0.79	8.3
Nyssa sylvatica	91	170	1.03	4.6	88	100	1.12	4.7	82	91	1.29	5.4
Liriodendron tulipifera	47	171	0.69	4.0	54	65	1.51	4.5	54	41	2.08	4.9
Hamamelis virginiana	42	157	0.33	3.1	39	70	0.17	2.2	37	55	0.15	2.3
Quercus velutina	68	58	1.01	2.7	62	30	1.39	3.4	40	14	0.99	2.1
Quercus rubra	57	50	0.88	2.4	62	32	1.85	4.3	55	24	2.43	4.8
Robinia pseudoacacia	82	72	0.57	2.2	64	26	0.70	2.0	58	19	0.68	1.8
Oxydendrum arboreum	79	80	0.45	2.1	79	82	1.08	4.2	81	73	1.50	5.1
Quercus alba	42	54	0.62	2.0	40	28	0.83	2.3	32	15	0.84	1.9
Castanea pumila	44	99	0.22	2.0	23	16	0.03	0.5	16	8	0.02	0.3
Pinus rigida	26	26	0.81	1.9	23	23	0.92	2.3	19	10	0.51	1.2
Betula lenta	32	57	0.36	1.6	46	53	0.70	2.7	48	39	0.97	3.0
Tsuga canadensis	16	13	0.25	0.7	42	66	0.71	3.1	50	71	1.17	4.5

Species nomenclature follows Kirkman et al. (2007). Density and basal area were calculated from trees >1.37 m height and ≥2.5 cm dbh (diameter at 1.37 m height). Only species with an IV of ≥2.0 in any sample period were included in the table; minor species with an IV < 2.0 were *Fraxinus americana*, *Betula alleghaniensis*, *Magnolia fraseri*, *Sassafras albidum*, *Diospyros virginiana*, *Magnolia acuminata*, *Prunus serotina*, *Aesculus octandra*, *Acer saccharum*, *Fagus grandifolia*, *Quercus falcata*, *Alnus serrulata*, *Ilex opaca*, *Pinus strobus*, *Acer pensylvanicum*, *Amelanchier arborea*, and *Tilia americana*

Table 2 Average density, basal area, species richness (S), Shannon's Index of diversity based on density (H′ density) and basal area (H′ basal area) for inventory periods in 1934–1935, 1969–1972, and 1988–1993 for the Coweeta Basin

|	1934–1935	1969–1972	1988–1993
Density (stems ha^{-1})	3121 a (89.4)	1886 b (58.1)	1372 c (40.0)
Cut stumps (stems ha^{-1})	209 (8.4)		
Basal area (m^2 ha^{-1})	27.98 a (0.65)	26.96 a (0.55)	30.69 b (0.68)
Cut stumps (m^2 ha^{-1})	6.92 (0.61)		
Richness (# species plot^{-1})	14.0 a (0.16)	14.0 a (0.17)	13.4 b (0.17)
H′ density	2.068 a (0.015)	2.119 b (0.015)	2.093 ab (0.017)
E density	0.784	0.803	0.807
H′ basal area	1.756 a (0.019)	1.852 b (0.018)	1.843 b (0.017)
E basal area	0.666	0.702	0.710

Average density and basal area of cut stumps in 1934–1935 inventory

Within rows, values followed by different letters are significantly different ($P < 0.05$) based on repeated measures ANOVA (PROC GLM, SAS 1999). Standard errors are in parentheses. Cut stumps were not identified to species in the 1934 inventory

14% for Axis 2, and 50% for Axis 3 (cumulative $R^2 = 81.8\%$ for the first three ordination axes) (Table 3). When the secondary matrix was examined, Axis 1 was negatively correlated with elevation (Table 3, $R \geq 0.30$). Axis 2 was positively correlated with annual precipitation and elevation and

Fig. 1 Diameter size class distribution of select tree species for three inventory periods in the Coweeta Basin, Western North Carolina: (**a**) 1934–1935 survey; (**b**) 1969–1972 survey; and (**c**) 1988–1993 survey. Each stacked-bar graph has been split and presented on two different scales
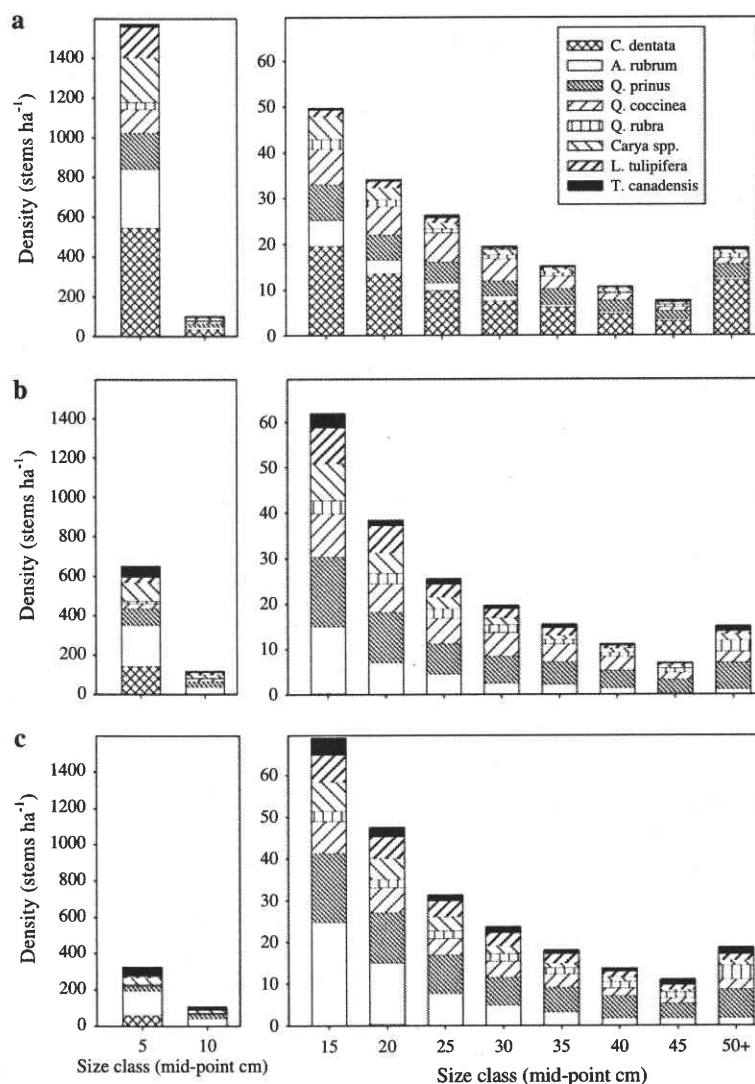
negatively correlated with solar radiation and soil clay content (Fig. 2b, Table 3). Axis 3 was positively correlated with basal area of cut stumps, soil organic matter, and A-horizon depth and negatively correlated with terrain shape, temperature, and modified azimuth (Fig. 2b, Table 3). In the NMS ordination diagram, tree species that were most positively related to Axis 1 were *T. canadensis*, *B. lenta*, and *Q. alba* (Table 4, tau ≥ 0.30); and species most negatively related were *Q. prinus* and *Q. rubra* (Fig. 2b, Table 4). The species most positively related to Axis 2 was *Q. prinus*; and species most negatively related were *Q. velutina*, *Cornus florida*, and *Q. alba*. The species most positively related to Axis 3 were *L. tulipifera*, *B. lenta*, *Q. rubra*, *Tilia*

americana, *Fraxinus americana*, and *Acer rubrum*; and the species most negatively related were *Q. coccinea*, *Pinus rigida*, *Castanea pumila*, and *Q. prinus* (Fig. 2b, Table 4).

The NMS ordination for the 1990s data (Fig. 2c) converged on three axes for the final solution (McCune and Mefford 1999). The final stress for the three-dimensional solution was 15.92. The proportion of variance explained was 12% for Axis 1, 32% for Axis 2, and 37% for Axis 3 (cumulative $R^2 = 81.8\%$ for the first three ordination axes) (Table 3). When the secondary matrix was examined, Axis 1 was positively correlated with soil clay content and negatively correlated with elevation and precipitation (Table 3, $R \geq 0.30$). Axis 2 was

a

b

c
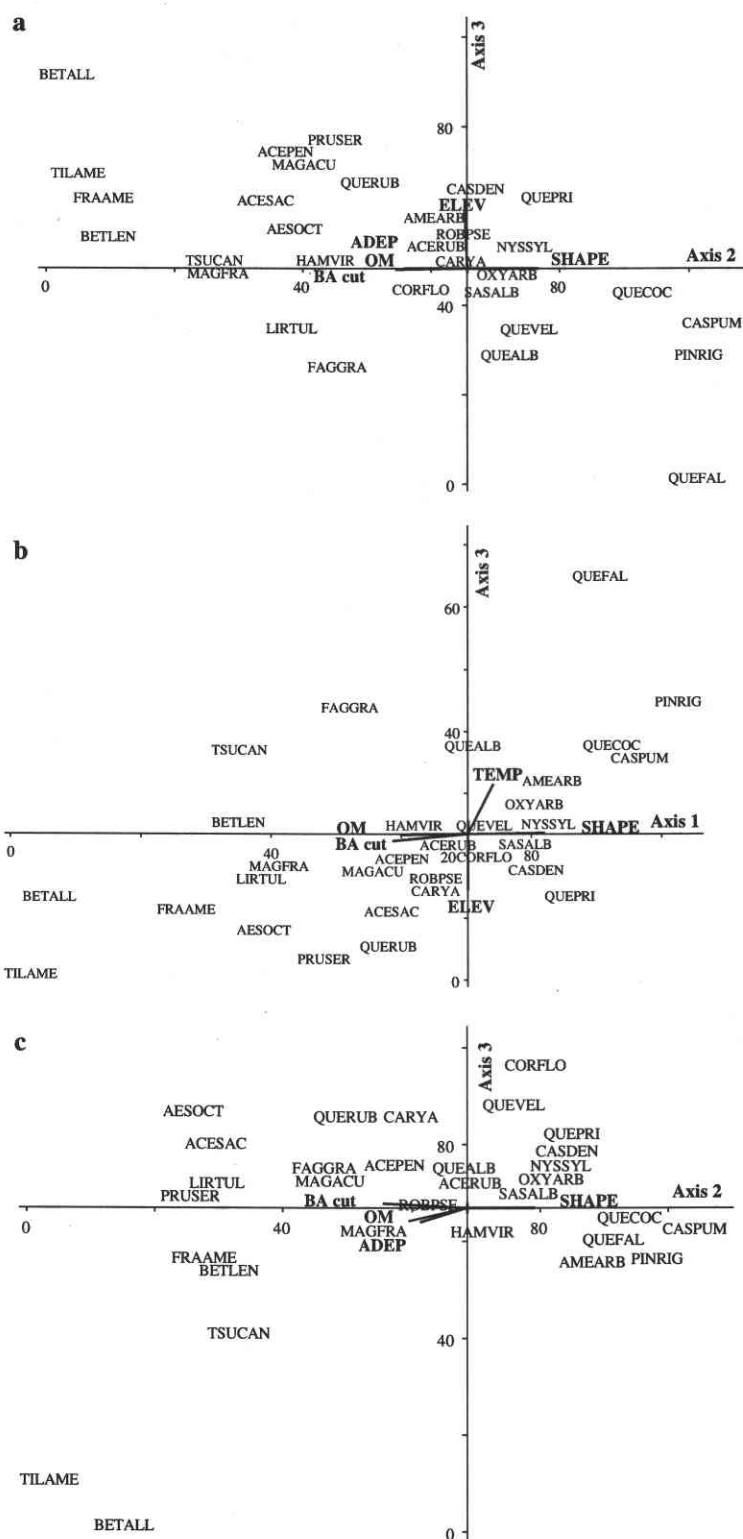
◀ **Fig. 2** Coweeta Basin, Western North Carolina for inventory periods: (**a**) 1934–1935, (**b**) 1969–1972, and (**c**) 1988–1993; nonmetric multidimensional scaling ordination diagram of species scores and environmental variables. Species codes: ACEPEN = *Acer pensylvanicum*; ACERUB = *Acer rubrum*; ACESAC = *Acer saccharum*; AESOCT = *Aesculus octandra*; AMEARB = *Amelanchier arborea*; BETALL = *Betula alleghaniensis*; BETLEN = *Betula lenta*; CARYA = *Carya* spp.; CASDEN = *Castanea dentata*; CASPUM = *Castanea pumila*; DIOVIR = *Diospyros virginiana*; FRAAME = *Fraxinus americana*; FAGGRA = *Fagus grandifolia*; HAMVIR = *Hamamelis virginiana*; LIRTUL = *Liriodendron tulipifera*; MAGACU = *Magnolia acuminata*; MAGFRA = *Magnolia fraseri*; NYSSYL = *Nyssa sylvatica*; OXYARB = *Oxydendrum arboreum*; PINRIG = *Pinus rigida*; PRUSER = *Prunus serotina*; QUEALB = *Quercus alba*; QUECOC = *Quercus coccinea*; QUEPRI = *Quercus prinus*; QUERUB = *Quercus rubra*; QUEVEL = *Quercus velutina*; ROBPSE = *Robinia pseudoacacia*; SASALB = *Sassafras albidum*; TILAME = *Tilia americana*; TSUCAN = *Tsuga canadensis*. Environmental codes: SHAPE = Terrain shape index; OM = soil organic matter content; BA cut = basal area of cut stumps; ELEV = elevation; TEMP = mean annual temperature; and ADEP = soil A-horizon depth. Only environmental variables with an $r^2 \geq 0.15$ were included in the ordination diagram. The two axes that explained the most variation are shown for each inventory period. Axes are displayed using "proportion of maximum" feature in PC-ORD and rotated using terrain shape in the secondary matrix to create better uniformity among the NMS graphical displays of the three inventory periods

positively correlated with basal area of cut stumps and negatively correlated with terrain shape. Axis 3 was positively correlated with soil organic matter, A-horizon depth, basal area of cut stumps, and negatively correlated with terrain shape (Fig. 2c, Table 3). In the NMS ordination diagram, the tree species most positively related to Axis 1 were *Q. alba*, *P. rigida*, and *Q. coccinea*; and the species most negatively related to that axis was *Q. prinus* (Fig. 2c, Table 4). The species most positively related to Axis 2 were *Carya* spp., *L. tulipifera*, and *Q. rubra*; and the species most negatively related were *Amelanchier arborea*, *P. rigida*, *Q. coccinea* (Fig. 2c, Table 4). Species that were most positively related to Axis 3 were *B. lenta*, *Tsuga canadensis*, *Tilia americana*, *L. tulipifera*, and *B. alleghaniensis*; and species most negatively related were *Q. prinus*, *Q. coccinea*, *Oxydendrum aboreum*, and *Nyssa sylvatica* (Fig. 2c, Table 4).

In the combined NMS analysis (all three inventory periods) (Fig. 3), the final stress for the three-dimensional solution was 16.56. The proportion of

variance explained was 34% for Axis 1, 16% for Axis 2, and 28% for Axis 3 (cumulative $R^2 = 78.3\%$ for the first three ordination axes) (Table 3). In the combined NMS analysis, plots moved across ordination space from the upper left coordinate in the ordination diagram in 1934 (Fig. 3) toward the lower right coordinate for the 1970s and 1990s inventory periods (Fig. 3). A clear separation emerged between 1934 plots and those from the 1970s and 1990s, while the 1970s and 1990s plots overlapped. The site variables most positively correlated to Axis 1 were soil organic matter, A-horizon depth, and basal area of cut stumps and the variable most negatively correlated was terrain shape (Table 3, $R \geq 0.30$). Axis 2 was positively correlated with temperature and soil clay content; and negatively correlated with elevation and annual precipitation. Axis 3 was positively correlated with basal area of cut stumps; and negatively correlated with terrain shape (Table 3, $R \geq 0.30$).

Tree species composition differed significantly among the three survey periods (MRPP; $T = -167.57$, $A = 0.077$, $P < 0.0001$). In addition, average distance increased from 1934 to the 1970s indicating greater within-group heterogeneity through time. Based on Sørensen distance measures, average within-group distance was 0.592 for 1934, 0.652 for the 1970s, and 0.644 for the 1990s. Multiple pair-wise comparisons showed significant differences between 1934 and the 1970s ($T = -151.16$, $A = 0.077$, $P < 0.0001$) and the 1990s ($T = -184.51$, $A = 0.094$, $P < 0.0001$); and a significant, although smaller difference between the 1970s and the 1990s ($T = -10.20$, $A = 0.050$, $P < 0.0001$).

Discussion

The loss of native species due to introductions of exotic pests and pathogens can alter long-term community and ecosystem dynamics (Ellison et al. 2005). The effects of large scale logging and the chestnut blight pandemic that co-occurred across eastern North America in the early 20th century are difficult to separate; however, it is important to examine the combined influences of these disturbance events on forest dynamics. In this study, we used long-term permanent plot data and multivariate analyses to evaluate the changes in species-

Table 3 Nonmetric multidimensional scaling (NMS) correlations for the 12 site variables with the first three ordination axes of vegetation data from inventories in 1934–1935, 1969–1972, and 1988–1993 in the Coweeta Basin

	Axis 1		Axis 2		Axis 3	
	r	tau	*r*	tau	*r*	tau
Inventory 1934–1935						
Slope	0.126	0.071	0.038	0.016	0.244	0.143
Elevation	0.030	0.008	−0.073	0.024	0.481	0.299
Terrain shape	0.282	0.184	**0.470**	0.358	−0.016	−0.040
Modified azimuth	0.156	0.099	0.291	0.207	−0.229	−0.171
Soil organic matter	0.046	0.048	**−0.438**	−0.321	0.025	0.067
Soil clay content	−0.084	−0.067	0.268	0.174	−0.231	−0.174
Soil depth	0.030	0.052	−0.200	−0.182	0.022	0.029
Soil A-horizon depth	0.033	0.025	**−0.409**	−0.318	0.033	0.049
Temperature	0.117	0.082	**0.301**	0.209	−0.263	−0.170
Solar radiation	0.123	0.084	0.289	0.184	**−0.310**	−0.206
Annual precipitation	0.077	0.059	−0.218	−0.103	**0.322**	0.185
Basal area of cut stumps	−0.107	−0.079	**−0.470**	−0.326	−0.027	−0.045
Coefficients of determination	0.191		0.376		0.297	
Cummulative % variance explained	19.1		56.7		86.5	
Final stress of 3-dimensional solution	15.063					
Inventory 1969–1972						
Slope	−0.236	−0.145	0.197	0.119	−0.015	−0.014
Elevation	**−0.377**	−0.272	**0.375**	0.201	0.143	0.001
Terrain shape	−0.180	−0.095	0.070	0.033	**−0.460**	−0.358
Modified azimuth	0.135	0.091	−0.144	−0.100	**−0.335**	−0.225
Soil organic matter	0.175	0.039	0.146	0.153	**0.423**	0.312
Soil clay content	0.161	0.139	**−0.311**	−0.253	−0.248	−0.151
Soil depth	0.110	−0.265	0.181	0.162	0.236	0.198
Soil A-horizon depth	0.183	0.093	0.126	0.115	**0.383**	0.295
Temperature	0.236	0.155	−0.118	−0.060	**−0.359**	−0.234
Solar radiation	0.068	0.035	**−0.327**	−0.214	−0.285	−0.179
Annual precipitation	−0.114	−0.096	**0.398**	0.240	0.241	0.104
Basal area of cut stumps	0.095	0.041	−0.134	−0.099	**0.477**	0.299
Coefficients of determination	0.176		0.140		0.502	
Cummulative % variance explained	17.6		31.6		81.8	
Final stress of 3-dimensional solution	15.494					
Inventory 1988–1993						
Slope	−0.217	−0.140	−0.013	−0.008	−0.081	−0.045
Elevation	**−0.441**	0.269	−0.024	−0.034	0.040	−0.09
Terrain shape	0.012	0.020	**−0.373**	−0.287	**−0.375**	−0.299
Modified azimuth	0.247	0.160	−0.252	−0.173	−0.186	−0.112
Soil organic matter	−0.163	−0.174	0.236	0.193	**0.449**	0.250
Soil clay content	**0.374**	0.293	−0.095	−0.060	−0.177	−0.072
Soil depth	−0.122	−0.111	0.120	0.108	0.272	0.176
Soil A-horizon depth	−0.134	−0.125	0.191	0.171	**0.422**	0.277
Temperature	0.297	0.180	−0.251	−0.176	−0.169	−0.091
Solar radiation	0.284	0.179	−0.107	−0.070	−0.249	−0.161

Table 3 continued

	Axis 1		Axis 2		Axis 3	
	r	tau	r	tau	r	tau
Annual precipitation	**−0.339**	−0.216	0.013	0.013	0.253	0.094
Basal area of cut stumps	−0.089	−0.02	**0.511**	0.330	**0.334**	0.181
Coefficients of determination	0.121		0.323		0.374	
Cummulative % variance explained	12.1		44.4		81.8	
Final stress of 3-dimensional solution	15.923					
All inventories combined						
Slope	−0.118	−0.075	−0.204	−0.135	−0.047	−0.029
Elevation	−0.035	−0.100	**−0.425**	−0.252	−0.012	−0.065
Terrain shape	**−0.337**	−0.238	0.114	0.091	**−0.375**	−0.266
Modified azimuth	−0.150	−0.087	0.282	0.182	−0.210	−0.129
Soil organic matter	**0.354**	0.207	−0.141	−0.155	0.260	0.172
Soil clay content	−0.124	−0.052	**0.317**	0.239	−0.080	−0.025
Soil depth	0.198	0.139	−0.077	−0.088	0.127	0.100
Soil A-horizon depth	**0.328**	0.213	−0.105	−0.101	0.241	0.184
Temperature	−0.149	−0.089	**0.386**	0.240	−0.216	−0.130
Solar radiation	−0.142	−0.082	0.261	0.165	−0.143	−0.083
Annual precipitation	0.143	0.044	**−0.304**	−0.188	0.046	−0.005
Basal area of cut stumps	**0.301**	0.191	−0.153	−0.073	**0.410**	0.235
Coefficients of determination	0.340		0.163		0.279	
Cummulative % variance explained	34.0		50.3		78.3	
Final stress of 3-dimensional solution	16.564					

Pearson's parametric (r) and Kendall's non-parametric (tau) correlations with ordination axes, $n = 281$. Environmental variables with $r \geq 0.30$ are highlighted in bold. Monte Carlo Test for stress in real data was $P < 0.02$ for all axes shown

environment relationships as affected by the loss of a canopy dominant, *Castanea dentata*, across a complex spatial and temporal gradient. In a previous study, Elliott et al. (1999) described seven vegetation community types that occur across elevation and topographic positions within the Coweeta Basin. Transitions between the different community types were considered gradual (Day and Monk 1974; Elliott et al. 1999) and thought to reflect gradients in species distribution (*sensu* Whittaker 1956) rather than distinct communities (Bolstad et al. 1998a; Elliott et al. 1999). We hypothesized that tree species distribution patterns overtime are attributed to the combined effects of environment and major disturbances of harvesting and the chestnut blight pandemic.

Harvesting of large trees from the late 1800s to the early 1900s was common across the southern Appalachian region (Brose et al. 2001). *Castanea dentata*

was harvested preferentially because it yielded valuable timber and was a good source of tannic acid (Frothingham 1924; Steer 1948). Douglass and Hoover (1988) estimated that more than 8 million board feet of timber were removed from the Coweeta Basin from 1919 to 1923. On the basis of cut stump data from the 1934 survey, we estimated that an average of 20% of the basal area was removed from the Basin. Thus, in 1934, the Coweeta Basin forest was in a recently disturbed condition and was recovering from logging. Many small stems were present at that time, and this suggests that the forest was then in the initiation stage of stand development (Oliver and Larson 1996). Average basal area in the Basin at the time of the first survey was nearly as low as that in a relatively young (17-year-old clearcut) forested watershed in the Coweeta Basin (Elliott et al. 1997). In 1923, the US Forest Service took over administration of the recently logged area and no

Table 4 Nonmetric multidimensional scaling (NMS) correlations for the tree species variables with the first three ordination axes for inventories in 1934–1935, 1969–1972, and 1988–1993

Species	1934–1935			1969–1972			1988–1993		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Acer pensylvanicum	−0.050	**−0.399**	0.165	−0.026	0.049	0.295	−0.114	0.300	0.192
Acer rubrum	−0.135	0.051	0.032	−0.027	0.145	0.302	−0.232	0.170	0.075
Acer saccharum	−0.106	−0.173	0.129	−0.111	0.041	0.164	−0.158	0.235	0.194
Aesculus octandra	0.120	−0.269	0.051	0.036	−0.036	0.276	−0.031	0.258	0.186
Amelanchier arborea	0.081	0.068	0.068	0.030	0.129	−0.243	0.061	**−0.379**	−0.083
Betula alleghaniensis	0.016	−0.247	0.109	0.047	0.196	0.290	−0.094	0.081	0.266
Betula lenta	0.003	**−0.493**	0.009	0.207	0.087	**0.487**	−0.133	**0.346**	**0.445**
Carya spp.	−0.249	−0.177	−0.022	−0.103	**−0.392**	0.204	0.154	**0.340**	−0.062
Castanea dentata	**−0.551**	−0.133	**0.604**	−0.200	−0.104	−0.140	0.027	−0.113	**−0.310**
Castanea pumila	0.139	**0.552**	−0.194	0.034	−0.039	**−0.350**	0.119	**−0.315**	−0.191
Cornus florida	−0.157	−0.269	−0.176	0.011	**−0.365**	0.159	0.230	0.239	−0.094
Fraxinus americana	0.013	**−0.428**	−0.045	0.053	−0.069	0.268	0.001	0.191	0.153
Hamamelis virginiana	0.088	−0.292	−0.021	0.143	0.183	0.189	−0.059	0.009	0.204
Liriodendron tulipifera	−0.142	**−0.534**	−0.101	0.128	−0.202	**0.517**	0.056	**0.497**	**0.402**
Magnolia acuminata	−0.135	−0.171	0.134	−0.026	0.004	0.235	−0.066	0.221	0.162
Magnolia fraseri	−0.014	−0.266	0.033	0.142	0.125	0.194	0.074	0.042	0.189
Nyssa sylvatica	0.164	0.245	−0.086	−0.022	0.112	−0.244	−0.054	−0.263	**−0.310**
Oxydendrum arboreum	−0.002	0.120	−0.090	0.069	−0.024	−0.221	0.132	−0.149	−0.225
Pinus rigida	0.118	**0.447**	−0.291	0.170	−0.064	**−0.480**	0.265	**−0.376**	−0.153
Prunus serotina	−0.071	−0.240	0.155	−0.059	0.020	0.153	−0.179	0.223	0.080
Quercus alba	−0.090	0.064	**−0.362**	0.368	**−0.346**	−0.095	**0.425**	−0.021	0.085
Quercus coccinea	0.243	**0.647**	−0.238	0.156	−0.147	**−0.650**	0.330	**−0.515**	**−0.315**
Quercus prinus	0.258	0.297	**0.329**	**−0.638**	0.289	−0.236	**−0.477**	−0.098	**−0.503**
Quercus rubra	−0.178	**−0.438**	0.285	−0.219	0.056	**0.386**	−0.208	**0.462**	0.169
Quercus velutina	−0.033	0.189	−0.284	0.045	**−0.457**	−0.056	0.258	0.015	−0.263
Tilia americana	0.077	**−0.314**	−0.046	0.060	−0.019	**0.308**	−0.122	0.266	**0.319**
Tsuga canadensis	0.063	**−0.373**	−0.131	**0.304**	−0.000	**0.377**	−0.025	0.223	**0.383**

Species not included in table with rank correlations less than 0.20 for any axis and sample period were *Fagus grandifolia*, *Quercus falcata*, *Robinia pseudoacacia*, and *Sassafras albidum*

Kendall's non-parametric (tau) correlations with ordination axes, $n = 281$. Species variables with tau $\geq$ 0.30 are highlighted in bold

further logging was done except in the experimental watersheds (not included in these data). By the time of the 1934 survey, the forest had only 10 years to recover from logging before the chestnut blight induced mortality of virtually all remaining chestnut trees. Unfortunately, no species-specific information is available about the trees removed during the 1919–1923 harvesting period as cut stumps were not identified to species on the 1934 survey sheets. Since *C. dentata* and *Quercus* species were the preferred commercial trees (Ashe 1911), we assumed that these species were selectively cut from the forest. From 1934 to the 1970s, density decreased by 40% and basal area by 3.6% as the forest matured and natural thinning proceeded during the stem exclusion stage of stand development (Oliver and Larson 1996). Between the 1970s and 1990s, density decreased by another 27% and basal area increased by 14%. Much of this increased basal area growth was attributed to two species, *Q. prinus* and *A. rubrum*.

In 1934, *C. dentata* was the dominant or co-dominant species (high frequency, density and basal area) across the environmental gradient; however, it was the most abundant at higher elevation (i.e., based

Fig. 3 Coweeta Basin, western North Carolina; nonmetric multidimensional scaling ordination diagram of plot scores using combined vegetation data for inventory periods 1934–1935, 1969–1972, and 1988–1993. Axis 1 and Axis 3 are displayed because they explain more of the variation in the NMS results than Axis 2 (see Table 4)
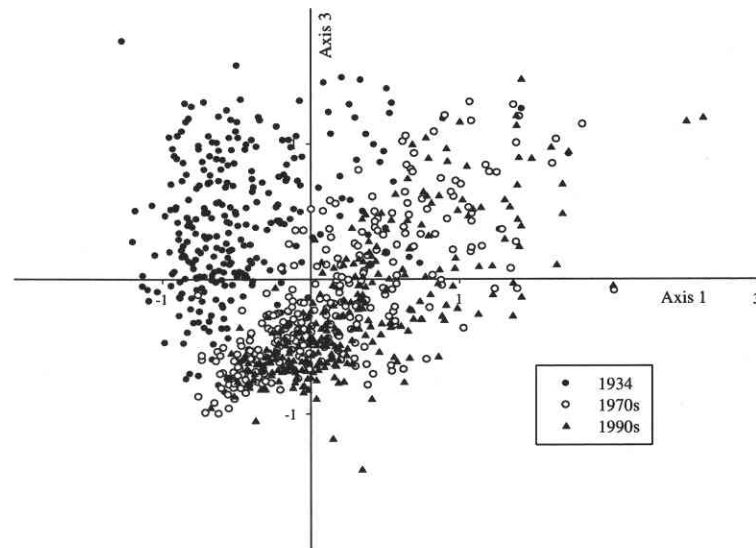
NMS ordination for 1934). Many small *C. dentata* stems were present in 1934 indicating successful recruitment following the earlier harvest and it also had more large stems than other species at that time. Based on the diameter distribution that remained after the harvesting between 1919 and 1923, we propose that *C. dentata* would have continued its dominant position in the forest in the absence of further disturbance. However, the chestnut blight pandemic dramatically altered this successional trajectory. By the 1970s, only sprouting stems of *C. dentata* remained in the forest due to chestnut blight induced mortality. Another less dramatic, yet significant, decline in *C. dentata* density occurred between the 1970s and 1990s. *Castanea dentata* sprouts remain a major component of some forests through a cycle of sprouting, blight infection, and dieback, which has persisted for decades (Stephenson 1986; Paillet 1988; Stephensen et al. 1991; Griffin 1989, 1992; Parker et al. 1993; Schwadron 1995).

In our study, the decline in density between the 1970s and 1990s suggests that *C. dentata* sprouting ability has decreased. Parker et al. (1993) attributed an observed decline in the number of sprouting *C. dentata* stems in southwestern Virginia to the interaction of continuing chestnut blight infection and drought between 1983 and 1988. The same phenomena are likely responsible for the decline in *C. dentata* sprouts in the Coweeta Basin. As the sprouting stems of *C. dentata* continued to decline from the 1970s to 1990s, co-occurring species became more abundant, replacing the formerly dominant overstory tree.

The NMS ordination results allowed us to interpret where species were located across the environmental gradient. Some species replaced *C. dentata* in specific environmental conditions, while others responded to the loss of *C. dentata* across environmental conditions. *Tsuga canadensis* increased in abundance (density and basal area) and distribution (frequency) between 1934 and the 1970s. Its increase was most notable near streams (low terrain) at low- to mid-elevations. Since *T. canadensis* is a shade tolerant species (Burns and Honkala 1990), it may have been present as saplings <2.5 cm dbh at the time of the 1934 inventory and not recorded, or it may have recruited into new areas by seed dispersal. However, observations at the time of the 1970s inventory (W.T. Swank, personal observation) point to recruitment by seed dispersal as the explanation of the increase in frequency and abundance of *T. canadensis*.

Early successional, disturbance adapted species, such as *L. tulipifera*, and *R. pseudoacacia* (Phillips and Shure 1990; Elliott et al. 1998), had high density and high numbers of small stems in the 1934 survey and *L. tulipifera* was associated with a high level of cutting (i.e., BA cut in the NMS ordination). They both declined in numbers in the later surveys. However, *Liriodendron tulipifera* increased in size and basal area over time, whereas *R. pseudoacacia* declined overall by the 1990s. *Liriodendron tulipifera* occurred primarily in moist coves, which are

characterized by low terrain shape and high organic matter content, at low- to mid-elevations (i.e., high association with axes 2 and 3 in the NMS ordination). In contrast, *Q. prinus* and *A. rubrum* were ubiquitous (high frequency and abundance), much like *C. dentata* before the chestnut blight, becoming dominant species across all environmental conditions.

Quercus species responded differently overtime to canopy gaps creation. Between 1934 and 1970s, all of the *Quercus* species (*prinus, coccinea, velutina, rubra,* and *alba*) increased in importance value and basal area primarily due to the canopy openings created by mortality of *C. dentata. Quercus* species most likely filled in gaps where they were already present, since their frequency did not increase between the first and second inventories. *Quercus rubra* increased in basal area in coves and mesic slope positions (low terrain shape), with high soil organic matter content. Between the 1970s an 1990s, *Q. prinus* and *Q. rubra* continued to increase in basal area and remained about the same in importance value, however, *Q. rubra* declined in frequency. In contrast, *Q. coccinea* and *Q. velutina* decreased in all estimates of abundance (i.e., frequency, basal area, and importance value). The species-specific responses to the drought that occurred from 1985 to 1988 may partially explain differences among *Quercus* in long-term changes. For example, Clinton et al. (1993) found that 83% of the canopy gaps in the Coweeta Basin were formed by *Quercus* during this drought and the most frequent gap-forming species were *Q. coccinea* (44%), *Q. rubra* (16%), *Q. velutina* (11%), *Carya* spp. (11%), and *Q. prinus* (7%). In our study, *Q. coccinea* was found on upper slopes and dry ridges (high terrain shape) where drought effects would be most extreme.

We attributed the significant increase in diversity ($H'_{basal\ area}$) from 1934 through the 1990s to the increase in evenness ($E_{basal\ area}$) of species distribution, since species richness decreased and average basal area increased. The canopy dominant, *C. dentata* was replaced by more than one species across the environmental gradient. *Quercus prinus, A. rubrum, C. florida, T. canadensis,* and *Oxydendrum arboreum* increased by 2–5% in importance value across the basin following the decline of *C. dentata,* and many other species increased by 1.0%.

We found that average distance in the NMS ordination was significantly (i.e., results from MRPP

separation test) greater for plots in the 1970s and 1990s than for plots in 1934, which suggests that species diversity was greater after *C. dentata* decline across the landscape (Palmer 1993). It is not surprising that species diversity increased after the virtual loss of *C. dentata* as this species was overwhelmingly dominant in 1934. Thus, the increase in diversity is attributable to a change in evenness of species distribution rather than an increase in species richness. The harvesting in the early 1900s coupled with the decline of *C. dentata* enhanced the general landscape pattern of diversity (i.e., NMS ordination, plots in 1934 vs. the 1970s and 1990s).

In addition to chestnut blight, other diseases and insects have been significant factors in the dynamics of vegetation in the Southern Appalachians. Studies have shown that the regional climate is extremely conducive to disease development and the incidence of disease and mortality in the Coweeta Basin is high (Chellemi et al. 1992; Britton 1993). For example, we recorded a decline in *C. florida* between the 1970s and 1990s. This decline of *C. florida* was strongly influenced by dogwood anthracnose caused by *Discula destructiva* Redlin, a serious disease in Southern Appalachian forests since about 1985 (Anderson 1991; Redlin 1991). Mortality of *R. pseudoacacia* was attributed to the locust borer (*Megacyllene robiniae*), which commonly infests young *R. pseudoacacia* in the Southern Appalachians (Boring and Swank 1984). However, none of these examples was as widespread and catastrophic as the functional loss of *C. dentata* due to the chestnut blight pandemic.

The invasion of the chestnut blight fungus did have a biologically significant impact on the Eastern deciduous forests as a whole (*sensu* Parker et al. 1999). The mortality and growth of the individual species, *C. dentata*, were affected dramatically as is shown by our data and that of others. Population abundance and dynamics of the species have shifted; our study shows that *C. dentata* abundance and distribution have been reduced substantially. The growth form has changed from a dominant tree to a small sprouting sapling, and the number of sapling sprouts has declined over time. The structure and diversity of forests have been altered through replacement of *C. dentata* by species with varying physiological and morphological characteristics. *Tsuga canadensis*, previously unimportant in the canopy, has emerged and become increasingly

important, particularly near stream channels at low-to high-elevations. *Liriodendron tulipifera* has recruited into moist coves at low-elevations and co-occurs with the ubiquitous *Q. prinus* and *A. rubrum*. *Quercus prinus* and *A. rubrum*, co-dominant species before the blight, tended to fill in the available space across all environmental conditions. The phenotypic and genotypic characters of *C. dentata* have undoubtedly changed. For decades, *C. dentata* has succumbed to the fungus before it could flower or produce seed; thus, much of the potential genetic composition of the species has been lost or stagnant. In addition, the preponderance of the research on *C. dentata* has been directed to the development of hybrids for the reintroduction of the species (Forest et al. 1990; Hebard 2004; Jacobs 2007), and development and reintroduction of hybrids would obviously alter the genetic structure of the species. Ecosystem processes have likely changed with the demise of *C. dentata* and subsequent replacement of that species by others with different growth rates, litter qualities, and decomposition and nutrient cycling rates (Smock and MacGregor 1988; Rhoades 2007).

References

Anagnostakis SA (1987) Chestnut blight: the classical problem of an introduced pathogen. Mycologia 79:23–37

Anderson RL (1991) Results of the 1990 dogwood anthracnose impact assessment and pilot test in the Southeastern United States. USDA Forest Service, Southern Region Proc Rep R8-PR 20

Ashe WW (1911) Chestnut in Tennessee. Baird-Ward Printing, Nashville, Tennessee

Aughanbaugh JE (1935) Replacement of the chestnut in Pennsylvania. Pennsylvania Department of Forests and Waters Bulletin Number 54, Pennyslvania

Bolstad PV, Swank WT, Vose JM (1998a) Predicting southern Appalachian overstory vegetation with digital terrain data. Landscape Ecol 13:272–283

Bolstad PV, Swift LW, Collins F, Régnière J (1998b) Measured and predicted air temperatures at basin to regional scales in the southern Appalachian mountains. Agric For Meteorol 91:161–176

Boring LR, Swank WT (1984) The role of black locust (*Robinia pseudoacacia*) in forest succession. J Ecol 72:749–766

Braun EL (1940) An ecological transect of Black Mountain, Kentucky. Ecol Monogr 10:193–241

Braun EL (1950) Deciduous forests of Eastern North America. Hafner Publishing Company, New York

Britton KO (1993) Anthracnose infection of dogwood seedlings exposed to natural inoculum in western North Carolina. Plant Dis 77:34–37

Brose P, Schuler T, Van Lear D, Berst J (2001) Bringing fire back: the changing regimes of the Appalachian mixed-oak forests. J For 99:30–35

Burns RM, Honkala BH (1990) Silvics of North America. 2. Hardwoods. Agriculture Handbook 654. USDA Forest Service, Washington, DC

Burrough PA (1986) Principles of geographical information systems for land resources assessment. Clarendon Press, Oxford, UK

Chellemi DO, Britton KO, Swank WT (1992) Influence of site factors on dogwood Anthracnose in the Nantahala Mountain Range of western North Carolina. Plant Dis 76:915–918

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Austr J Ecol 18:117–143

Clinton BD, Boring LR, Swank WT (1993) Characteristics of drought-induced canopy gaps in oak forests of the Coweeta Basin. Ecology 74:1551–1558

Crowley PH (1992) Resampling methods for computation-intensive data analysis in ecology and evolution. Ann Rev Ecol Syst 23:405–447

Day FP, Monk CD (1974) Vegetation pattern on a Southern Appalachian watershed. Ecology 55:1064–1074

Day FP, Phillips DL, Monk CD (1988) Forest communities and patterns. In: Swank WT, Crossley DA (eds) Forest hydrology and ecology at Coweeta, ecological studies 66. Springer-Verlag, New York, pp 141–149

Douglass JE, Hoover MD (1988) History of Coweeta. In: Swank WT, Crossley DA (eds) Forest hydrology and ecology at Coweeta, Ecological Studies 66. Springer-Verlag, New York, pp 17–31

Elliott KJ, Boring LR, Swank WT, Haines BR (1997) Successional changes in plant species diversity and composition after clearcutting a southern Appalachian watershed. For Ecol Manage 92:67–85

Elliott KJ, Boring LR, Swank WT (1998) Changes in vegetation structure and diversity after grass-to-forest succession in a southern Appalachian watershed. Am Midl Nat 140:219–232

Elliott KJ, Vose JM, Swank WT, Bolstad PV (1999) Long-term patterns in vegetation-site relationships in southern Appalachian forests. J Torrey Bot Soc 126:320–334

Ellison AM, Bank MS, Barker-Plotkin AA, Clinton BD, Colburn BA, Elliott K, Ford CR, Foster DR, Jefts S, Kloeppel BD, Knoepp JD, Lovett GM, Malloway J, Mathewson B, McDonald R, Mohan J, Orwig DA, Rodenhouse NL, Sobczak WW, Stinson KA, Snow P, Stone J, Thompson J, Von Holle B, Webster JR (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Front Ecol Environ 3:479–486

Forest HS, Cook RJ, Bebee CN (1990) The American chestnut: a bibliography of references to *Castanea dentata* and other chestnut species, and on chestnut blight and its causal pathogen of the fungal genus *Endothia* or *Cryphonectria*. Bibliographies and Literature of Agriculture Number 103. USDA National Agricultural Library, Beltsville, Maryland

Frothingham EH (1924) Some silvicultural aspects of the chestnut blight situation. J For 22:861–872

Good NF (1968) A study of natural replacement of chestnut in six stands in the highlands of New Jersey. Bull Torrey Bot Club 95:240–253

Gravatt GF, Marshall RD (1926) Chestnut blight in the southern Appalachians. USDA Department Circular, Washington, DC

Griffin GJ (1989) Incidence of chestnut blight and survival of American chestnut in forest clearcut and neighboring understory sites. Plant Dis 73:123–2126

Griffin GJ (1992) American chestnut survival in understory mesic sites following the chestnut blight pandemic. Can J Bot 70:1950–1956

Hebard FV (2004) Notes from meadowview research farms. J Am Chestnut Found 18:38–59

Jacobs DF (2007) Toward development of silvical strategies for forest restoration of American chestnut (*Castanea dentata*) using blight-resistant hybrids. Biol Conserv 137:497–506

Karban R (1978) Changes in an oak-chestnut forest since the chestnut blight. Castanea 43:221–228

Keever C (1953) Present composition of some stands of former oak-chestnut forest in the Southern Blue Ridge mountains. Ecology 34:44–54

Kirkman LK, Brown CL, Leopold DJ (2007) Native trees of the Southeast. Timber Press Inc., Portland, Oregon

Knoepp JD, Swank WT (1997a) Long-term effects of commercial harvest on soil cation concentrations. For Ecol Manage 93:1–7

Knoepp JD, Swank WT (1997b) Forest management effects on surface soil carbon and nitrogen. Soil Sci Soc Am J 61:928–935

Korstian CR, Stickel PJ (1927) The natural replacement of blight-killed Chestnuts in the hardwood forests in the Northeast. J Agric Res 34:631–648

Mackey HE, Sivec N (1973) The present composition of a former oak-chestnut forest in the Allegheny Mountains of western Pennsylvania. Ecology 54:915–919

Magurran AE (2004) Measuring biological diversity. Blackwells, Oxford, UK

McCormick JF, Platt RB (1980) Recovery of an Appalachian forest following the chestnut blight. Am Midl Nat 104:264–273

McCune B, Mefford MJ (1999) PC-ORD multivariate analysis of ecological data, Version 4. MjM Software Design, Gleneden Beach, Oregon

McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon

McEwan RW, Rhoades C, Beiting S (2005) American chestnut (*Castanea dentata*) in the pre-settlement vegetation of Mammoth Cave National Park, central Kentucky, USA. Nat Areas J 25:275–281

Mielke PW (1991) The application of multivariate permutation methods based on distance functions in the earth sciences. Earth Sci Rev 31:55–71

Milgroom MG, Wang K, Zhou Y, Lapari SE, Kaneko S (1996) Intercontinental population structure of the chestnut blight fungus, *Cryphonectria parasitica*. Mycologia 88:179–190

McNab WH (1989) Terrain shape index: quantifying effects of minor landforms on tree height. For Sci 35:91–104

Myers BR, Walck JL, Blum KE (2004) Vegetation change in a former chestnut stand on the Cumberland Plateau of Tennessee during an 80-year period (1921–2000). Castanea 69:81–91

Nelson TC (1955) Chestnut replacement in the southern highlands. Ecology 36:352–353

Oliver CD, Larson BC (1996) Forest stand dynamics. McGraw-Hill, New York

Paillet FL (1988) Character and distribution of American chestnut sprouts in southern New England woodlands. Bull Torrey Bot Club 109:457–473

Parker GG, Hill SM, Kuehnel LA (1993) Decline of understory American chestnut (*Castanea dentata*) in a southern Appalachian forest. Can J For Res 23:259–265

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biol Invasions 1:3–19

Palmer MW (1993) Putting things in better order: the advantages of canonical correspondence analysis. Ecology 74:2215–2230

Phillips DL, Shure DJ (1990) Patch-size effects on early succession in Southern Appalachian forests. Ecology 71:204–212

Redlin SC (1991) *Discula destructiva* sp. nov., cause of dogwood anthracnose. Mycologia 83:633–642

Rhoades CC (2007) The influence of American chestnut (*Castanea dentata*) on nitrogen availability, organic matter and chemistry of silty and sandy loam soils. Pedobiologia 50:553–562

SAS Institute (1999) SAS system, version 8. SAS Institute, Cary, North Carolina

Schwadron PA (1995) Distribution and persistence of American chestnut sprouts, *Castanea dentata* (Marsh.) Borkh., in Northeastern Ohio woodlands. Ohio J Sci 95:281–288

Shugart JR, West DC (1977) Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the chestnut blight. J Environ Manage 5:161–175

Smith RN (1991) Species composition, stand structure, and woody detrital dynamics associated with pine mortality in the southern Appalachians. MS Thesis, University of Georgia, Athens, Georgia

Smock LA, MacGregor CM (1988) Impact of the American chestnut blight on aquatic shredding macroinvertebrates. J North Am Benthol Soc 7:212–221

Steer HB (1948) Lumber production in the United States 1799–1946. USDA, Miscellaneous Publication Number 669, Washington, DC

Stephenson SL (1986) Changes in a former Chestnut-dominated forest after a half century of succession. Am Midl Nat 116:173–179

Stephenson SL, Adams HS, Lipford ML (1991) The present distribution of chestnut in upland forest communities of Virginia. J Torrey Bot Soc 118:24–32

Swift LW (1968) Comparison of methods for estimating areal precipitation totals for a mountain watershed. Am Meteorol Soc Bull 49:782–783

Swift LW (1976) Algorithm for solar radiation on mountain slopes. Water Resources Res 12:108–112

Swift LW, Knoerr KR (1973) Estimating solar radiation on mountain slopes. Agric Meteorol 12:329–336

Swift LW, Cunningham GB, Douglass JE (1988) Climatology and hydrology. In: Swank WT, Crossley DA (eds) Forest hydrology and ecology at Coweeta, Ecological Studies 66. Springer-Verlag, New York, pp 35–55

Swift LW, Waide JB, White DL (1989) Refinements in the Z-T method of extreme value analysis for small watersheds. In: Proceedings of the Sixth Conference on Applied Climatology. American Meterological Society, Charleston, South Carolina, pp 60–65

ter Braak CJF (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167–1179

Thomas DJ (1996) Soil survey for Macon County, North Carolina. USDA Natural Resources Conservation Service, Raleigh, North Carolina

Van Lear DH, Vandermast DB, Rivers CT, Baker TT, Hedman CW, Clinton BC, Waldrop TA (2002) American chestnut, rhododendron, and the future of Appalachian cover forests. In: Outcalt KW (ed) Proceedings of the eleventh biennial southern silvicultural research conference, Gen Tech Rep SRS-48, USDA Forest Service, Southern Research Station, Asheville, NC, pp 214–220

Whittaker RH (1956) Vegetation of the Great Smoky Mountains. Ecol Monogr 26:1–80

Woods FW, Shanks RE (1957) Replacement of chestnut in the Great Smoky Mountains of Tennessee and North Carolina. J For 55:847

Woods FW, Shanks RE (1959) Natural replacement of chestnut by other species in the Great Smoky Mountains National Park. Ecology 40:349–361

Yeakley JA (1993) Hillslope soil moisture gradients in an upland forested watershed. PhD Dissertation, University of Virginia, Charlottesville, Virginia